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15 Lemur Hunting in Madagascar's Present and Past

The Case of *Pachylemur*

Natalie Vasey & Laurie R. Godfrey

Fihazana ny gidro tamin'ny fotoana taloha sy ankehitriny ao Madagasikara: Mahakasika manokana ny *Pachylemur*

Famintinana

Pachylemur dia gidro iray efa lany tamingana izay niparitaka be teto Madagasikara ary velona hatramin'ny 500 taona lasa izay. Mbola miteraka adihevitra lehibe momba ny andraikitry ny olombelona amin'ny fanjavonan'ny biby lehibe an'i Madagasikara. Eto izahay dia manombatombana ny fiantraikan'ny olombelona nalaina avy tamin'ny fikarohana momba ny fihazana lemur ankehitriny miaraka amin'ny porofo avy amin'ny tantara am-bava an'i Madagascar ary koa ireo firaketana arkeolojika sy paleontolojika. Ny gidro velona dia hazaina manerana an'i Madagasikara, indrindra eo amin'ny hahazoana fivelomana ary hamidy mba hampidi-bola. Ny fahantrana sy ny tsy fahampiantsakafo no mitarika fihinanana bibidia. Ny sata miaro, ny fady eo amin'ny fihinana ny bibidia, ary ny safidin'ny hena any an-toerana dia toa tsy ampy hanampiana ny fiarovana ny ankamaroan'ny taxa gidro tsy ho lany tamingana nohon'ny taha-mpamokarana misy any amin'ny faritra Makira, raha tsy any an-kafa. Ny fanazavana tokana amin'ny fahalanian-tamingan'ireo biby lehibe, toy ny famonoana haingana na ny fiovan'ny toetrandro, dia tsy ampy. Niara-niaina nandritran'ny fotoana maharitra ny olombelona sy ny *Pachylemur* teto Madagasikara. Tsy nisy haintany nanerana ny Nosy rehefa nanomboka ringana ny biby lehibe tokony ho 1200 taona lasa izay; ny faritra sasany eto madagasikara dia mando ary ny hafa kosa maina. Ny "isotope" maritoeran'ny azota ($\delta^{15}N$) ho an'ny taolan'ny *Pachylemur* nodatina tamin'ny radiocarbon dia tsy mampiseho porofo koa fa ny hain-tany dia nandray anjara tamin'ny fahafatesany. Taolana *Pachylemur* avy any amin'ny toeranm-pikaroana palezaolojika Tsirave dia mitombo isa maherin'ny 1 000 taona lasa izay, maneho ny fitrandrahana maharitra mandritra ny ~ 100 taona. *Pachylemur* dia misy toetra maro hitovizany tamin'ny havany akaiky indrindra, ny gidro miovaova (*Varecia*), anisan'izany ny ireo izay mihinana voankazo. Ny tantaram-bavan'ny biby heverina fa *Pachylemur* dia nonina tao amin'ireo ala misy hazo lehibe indrindra izy ary naneho fihetsika fanoherana mahery setra. Toa an'i *Varecia*, *Pachylemur* dia azo inoana fa niankina tanteraka tamin'ny hazo mamokatra voakazo ary manaparitaka tsara ny voankazo, ary mety hoan'ny fananahana koa (ohatra: mametraka akany ary mitahiry ny biby izay efa tsy mifikitra amin'ny reniny), izay mahatonga azy io ho mora tohina indrindra amin'ny fahasimban'ny toeram-ponenana. Noho izany dia namintina izahay fa ny fahasimban'ny toeram-ponenana sy ny fihazana dia samy nandray anjara tamin'ny famongorana an'i *Pachylemur*.

Teny fanalahidy

Bushmeat – gidro – lany tamingana – *Pachylemur* – *Varecia* – subfossiles

Abstract

Pachylemur is a large extinct lemur once widespread on Madagascar that survived in pockets until at least 500 years ago. The role of humans as agents of megafaunal extinction on Madagascar is heavily debated. Here we evaluate human impacts drawing from research on lemur hunting today combined with evidence from

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Madagascar's oral history as well as its archaeological and paleontological records. Living lemurs are hunted throughout Madagascar, primarily for subsistence but also for commercial trade. Wildlife consumption is driven primarily by poverty and resultant food insecurity. Protected status, wildlife consumption taboos, and broad preference for domestic meats appear insufficient to buffer most lemur taxa from extinction at current harvest rates in the Makira region, if not elsewhere. Single-factor explanations for megafaunal extinction, such as rapid overkill or climate change, are not viable. There was long temporal overlap for *Pachylemur* and humans on Madagascar. There was no island-wide drought when the megafauna began to crash around 1,200 years ago; some parts of Madagascar were unusually wet while others were unusually dry. Stable isotope ($\delta^{15}N$) values for radiocarbon-dated *Pachylemur* bones also show no evidence that aridification contributed to its demise. Butchered bones of *Pachylemur* from the paleontological site Tsirave spike in frequency just over 1,000 years ago, indicative of sustained exploitation over a ~100-year period. *Pachylemur* shared many traits with its closest living relative, variegated lemurs (*Varecia*), including frugivory. Oral histories of an animal presumed to be *Pachylemur* indicate it dwelt in the largest trees in the forest, was active at twilight, and exhibited highly aggressive antipredator behavior. Like *Varecia*, *Pachylemur* was likely dependent on large, patchily distributed trees for fruit, and possibly also for reproduction (e.g. to nest and stash non-clinging young), making it especially vulnerable to habitat degradation. We thus conclude that both habitat degradation and hunting played a role in the extinction of *Pachylemur*.

Key words Bushmeat, Lemurs, Extinction, *Pachylemur*, *Varecia*, Subfossils

15.1 Introduction: The Role of Humans as Agents of Megafaunal Extinction

In 2015, Radimilahy and Crossland reviewed the archaeological history of Madagascar, including evidence of early encounters of humans with now-extinct species. Since then, new data have emerged, provoking renewed debate over the time of initial arrival of humans to Madagascar. Some have argued that humans arrived over 10,000 years ago (Godfrey et al., 2019; Hansford et al., 2018), others by at least 2,000 years ago (Douglass et al., 2019a; Pierron et al., 2017; Wang et al., 2019), and still others not until ~1,500 years ago or later (Anderson et al., 2018; Mitchell, 2020). Debate also centers around the role of humans as agents of megafaunal extinction and how this relates to the timing of human arrival. For example, Godfrey et al. (2019) and Hansford et al. (2018) both argue that humans arrived early, but that early human populations had little or no impact on the megafauna: the megafaunal collapse occurred much later.

Some of the most provocative data come not from archaeological sites but from sites that yield paleontological and paleoecological (including paleohydrological) data, but no single record taken alone establishes a major role for humans as agents

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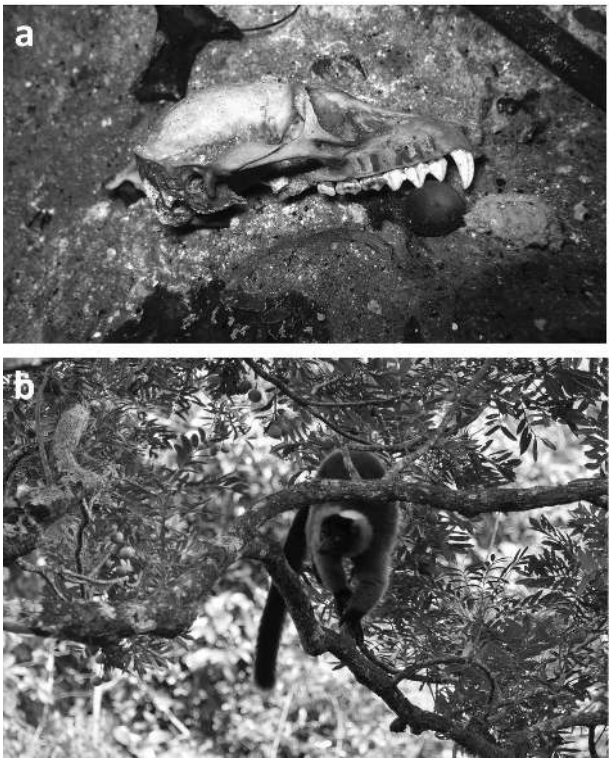

Figure 15.1 (a) *Pachylemur insignis* skull under water at Vintany Cave, Tsimanampesotse National Park, southwest Madagascar, 2016. Photograph by Barry Coleman. (b) *Varecia rubra* photographed from the forest canopy, Andranobe Forest, Masoala National Park, Madagascar, 2009. Photograph by Natalie Vasey.

of megafaunal extinction on Madagascar. Taken together, however, and in the context of understanding wild animal hunting on Madagascar today, an interesting, though complex, picture emerges. Here we focus on one extinct lemur, *Pachylemur* (Fig. 15.1a), an animal that may have survived in pockets on Madagascar until very recently, and for which clear evidence of butchery by humans occurs in the fossil record. *Pachylemur* was widespread across the island, large-bodied, and frugivorous, and presumably an important disperser of large seeds. We begin by reviewing wild animal hunting as part of the broader economy in Madagascar and continue by examining evidence from Madagascar's oral history as well as its archaeological and paleontological records.

15.2 Hunting Wild Animals as an Integral Part of the Human Diet in Madagascar

Irrespective of the debate over whether or not humans played a primary role in the extinction of Madagascar's megafauna and the impact of hunting (as opposed to

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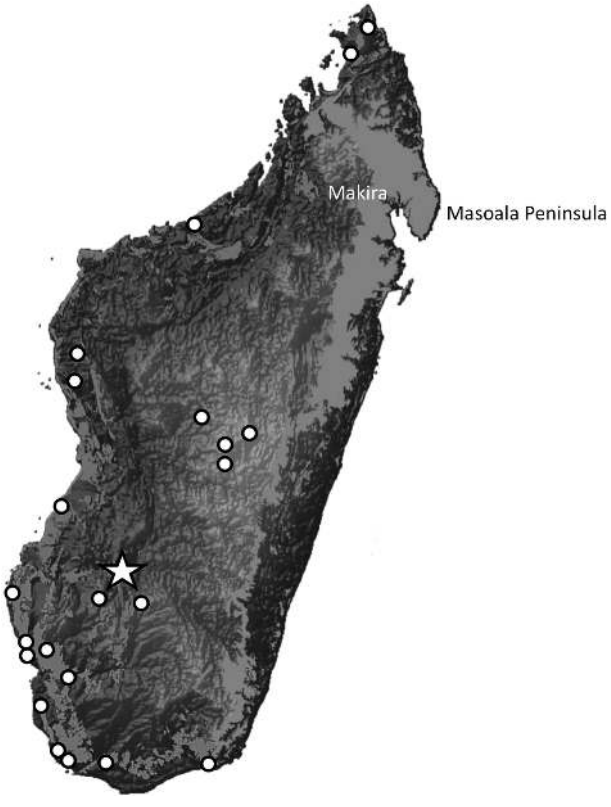

Figure 15.2 *Pachylemur* subfossil sites on Madagascar. White circles represent individual subfossil sites with *Pachylemur*; white star represents the subfossil site of Tsirave. The Masoala Peninsula and the Makira region are labeled; extensive research on the ecology, behavior, reproduction, and bushmeat hunting of *Varecia* have taken place in these regions.

other human activities) on large-bodied endemic species, it is certain that humans hunt lemurs and other wild animals in Madagascar today. From this standpoint, the debate over whether humans hunted lemurs in the remote past can appear belabored. We therefore begin by providing background on the hunting of lemurs today, particularly those that are the closest extant relatives of *Pachylemur*, that is, the variegated lemurs (*Varecia* spp.) (Fig. 15.1b). Variegated lemurs occur in the Makira region and on the Masoala Peninsula (Fig. 15.2) as well as in other rain forests in eastern Madagascar, although the subfossil record reveals they were previously much more widespread (Burney et al., 2020). They likely shared a host of ecological, behavioral, and reproductive characteristics with *Pachylemur*.

Madagascar today has an economy dominated by agropastoralism, but where hunting of wild animals is also routine. The vast majority of its people are rural; they grow rice and raise livestock, supplementing these with wild and other domesticated or cultivated foods. During the French colonial period, Decary (1939), administrative head of colonies, wrote at length about hunting and trapping of wild animals

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among native Malagasy, echoing the observations of Flacourt (1661) before him. Decary enumerated the wild animal species that were hunted, described and illustrated snares and other implements used for hunting, and even summarized motives: "The Malagasy do not take up hunting for pleasure or sport; above all they view this work as utilitarian which they carry out moreover to get rid of animals that are a nuisance (wild boar, crocodiles) as well as to obtain needed meaty nourishment (tenrecs, birds, bats) or to increase their herds (wild cattle)" (p. 3). The first section of Decary's article describes methods used to hunt lemurs, prefaced by an acknowledgment of how easy it is to extirpate them. After the colonial era, the hunting of wild animals in Madagascar became governed by a legal framework which classifies species as protected, game, or nuisance (Rakotoarivelo et al., 2011). "Protected" species cannot be killed or collected; "game" species can be hunted during a defined season for subsistence as long as certain methods are avoided; and "pest" species can be killed at any time by anyone.

From the late 1980s onward the Malagasy government began allowing wildlife researchers into the country after nearly two decades of limited interchange with the West following independence. Behavioral, ecological, and phylogenetic studies of lemurs and other wildlife flourished, much of it in the service of conservation. As a by-product, a considerable number of records concerning hunting and consumption of wild animals were published. Table 15.1 summarizes many of these early records for lemurs, documenting that they were being hunted throughout Madagascar despite being classified as protected. These records relied on interviews or bodily remains and spurred development of more systematic study, which began with the work of Golden (2009). Recent research on bushmeat hunting in Madagascar draws on a wide range of methodological approaches and incorporates conservation objectives as well as human livelihoods. Some of the current methods used to study wildlife hunting in Madagascar include structured household interviews, daily diet diaries, human health monitoring, interviews and observation of hunters, and direct recording by local monitors of bushmeat passing through villages and towns (e.g. Borgerson, 2015, 2016; Borgerson et al., 2016, 2018; Golden, 2009; Golden et al., 2011, 2013; Jenkins et al, 2011; Randrianandrianina et al., 2010; Razafimanahaka et al., 2012; Reuter et al., 2016a, 2016b).

Wild animals are hunted for two reasons, first for subsistence, to be consumed primarily by the hunters' households, and second for commercial trade. A prominent example of subsistence hunting comes from the Makira region in northeastern Madagascar where 98% of consumed wildlife was collected by the hunter and his family and the remaining 2% was purchased (Golden et al., 2014). In a village on the Masoala Peninsula (also in northeastern Madagascar), lemur trappers consumed all of the lemurs they had trapped; none were sold (Borgerson et al., 2016). A focal hunter did sell 24% (by biomass) of bush pig during the study year as this is the largest forest mammal, too large for his family alone to consume (Borgerson, 2016). The village lacked electricity and refrigeration, as do many villages throughout Madagascar. In contrast to these prominent examples of subsistence hunting, Reuter et al. (2016a) document that transport and trade of wild meats in

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Table 15.1 Records of lemur hunting (1995–2008) prior to systematic bushmeat research

Species	Location	Type of record	Reference
Daubentonia madagascariensis	Near Marojejy National Park (NE)	Bodily remains	Glaw et al. (2008)
Daubentonia madagascariensis	Near Ambanja village (N)	Bodily remains	Koenig and Zavasoa (2008)
Hapalemur occidentalis	Near Masoala National Park (NE)	Interviews	Martinez (2008)
Eulemur albifrons	Makira Natural Park (NE)	Interviews	Patel and Andrianandrasana (2008)
Varecia rubra *Varecia variegata subcincta*	Makira Natural Park (NE)	Interviews	Hekkala et al. (2007)
Lemur catta	Andohahela National Park (SE)	Bodily remains	Moniac and Heitman (2007)
Propithecus edwardsi *Varecia variegata variegata*	Fandriana Marolambo corridor (SE)	Interviews	Lehman et al. (2006)
Daubentonia madagascariensis	Near Betomendry village (NW)	Bodily remains	Koenig (2005)
Eulemur albifrons *Eulemur rubriventer* *Propithecus candidus*	Marojejy National Park (NE)	Interviews Bodily remains	Patel et al. (2005)
Eulemur rufifrons *Lemur catta* *Lepilemur ruficaudatus* *Propithecus verreauxi*	Kirindy-Mite National Park (SW)	Interviews Skeletal remains	Goodman and Raselimanana (2003)
Avahi occidentalis *Eulemur fulvus* *Lepilemur edwardsi* *Propithecus coquereli*	Ankarafantsika National Park (NW)	Skeletal remains	Garcia and Goodman (2003)
Lepilemur mustelinus *Propithecus edwardsi* *Varecia variegata variegata*	Fandriana Marolambo corridor (SE)	Interviews	Lehman and Ratsimabazafy (2001)
Daubentonia madagascariensis	Anjimangirana (NW - eaten); Various other sites – killed, not eaten	Interviews	Simons and Meyers (1991)
Eulemur coronatus *Eulemur sanfordi* *Lepilemur ankaranensis*	Daraina Forest fragments (N)	Interviews	Randrianarisoa et al. (1999)
Eulemur albifrons	Marojejy National Park (NE)	Interviews	Duckworth et al. (1995)

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Madagascar is often formalized (i.e., commercial), though hunting usually is not. Across a multitude of study locations between Antananarivo (central Madagascar) and Antsiranana (far north), both urban and rural people purchased a substantial proportion of the wild meat they consumed through third parties, though the majority was obtained for free by hunting or as gifts. Furthermore, a significant proportion of these wild animals were moved long distances using the intercity transit system and then sold at wild meat selling establishments, including market stalls and restaurants (Reuter et al., 2016a).

In some rural areas hunting is carried out primarily opportunistically during the course of other activities based around forest use. For example, in Ranobe in southwestern Madagascar, most villagers are farmers who have little time or reason to enter the forest regularly, but when they do they take a slingshot and a knife, and are thus prepared to capture animals to supplement their diet. Only a few individuals in Ranobe hunt regularly to generate an income; all of them have little land and are therefore unable to derive a livelihood through farming (Gardner & Davies, 2014). Similarly, at Ankarafantsika National Park in northwestern Madagascar, villagers feed on forest animals while collecting raffia palm (*Raffia farinara*). Raffia (used for weaving, building, and food) is harvested seasonally from forest-based camps. Rice is the only food brought to the forest and additional sustenance is obtained from hunting forest animals. At one such camp, butchered lemur skeletal remains were the most abundant based upon estimated minimum number of individuals (Garcia & Goodman, 2003).

In other rural areas, targeted hunting of wild animals is much more common. This is so in regions occupied by *Pachylemur*'s smaller-bodied relatives, *Varecia rubra* on the Masoala Peninsula and *Varecia variegata* in Makira. Here hunting may be targeted (e.g. using snares), opportunistic (e.g. using sling shots, rocks, or sticks), or incidental (i.e. by-catch). In one particular village on Masoala, 75% of households had hunted forest mammals and 22% had intentionally trapped lemurs in the year prior to the study. Thirty three percent of households reported having caught a lemur in the prior year and 26% of village men trapped lemurs (Borgerson et al., 2016). In a study involving over 600 households bordering Masoala National Park (13 villages) and Makira Natural Park (26 villages), 16% of households hunted bats, 23% hunted bush pigs, 40% hunted carnivores, 49% hunted lemurs, and 91% hunted tenrecids (Golden et al., 2014).

The methods used to trap lemurs in Decary's day, such as snare traps set within *laly*, are still in use today (Borgerson, 2015; Decary, 1939; Golden, 2009). A *laly* is a swath of cleared forest, either linear or circular, which lemurs cross via horizontally-placed "bridges" made of saplings on which snares are built. Unlike trapping sites for other forest mammals, *laly* are owned by the hunters who clear the land. Surrounding one small village on Masoala containing 36 households, there were 73 *laly* (Borgerson, 2015). One hunter owned 14 of these but used only three in the study year. Hunters rotate use of *laly* from year to year, pausing use when lemurs are depleted and the *laly* goes "fallow". They select *laly* to re establish the next year based on number of years since previous use and number of lemurs observed in the area. Hunters know their wild prey well and this knowledge dictates when and how they

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hunt particular types of prey in order to maximize catch. For example, on the Masoala Peninsula *Varecia rubra* and *Eulemur albifrons* are hunted primarily in the austral winter (Mar–Aug) when they are fatter and when their primary food trees are especially large. These trees can be isolated within circular *laly* laden with snare traps (Borgerson, 2016).

Although the number of households that hunt and consume wild animals can be considerable in any given rural area, terrestrial wild animals typically contribute a relatively small proportion of animal protein to the overall diet. For example, in the Aloatra-Mangoro region of eastern Madagascar, most meals (74.5%) contained no meat, 11.8% contained protein from domestic animals, and 13.7% contained protein from wild-caught animals (Jenkins et al., 2011). Most of the latter consisted of fish and invertebrates. Just 1.3% of meals were from terrestrial wild animals and just 0.5% included meat from legally protected species. During a year-long study in one village on the Masoala Peninsula, villagers ate just over one meal containing meat (wild or domestic) per day (1.29 $\pm$ SD 0.19) (Borgerson, 2016). During the austral summer more animal protein was consumed with 89% of meals containing fish, 9% domestic animals, and 2% forest mammals. The two most commonly eaten forest mammals in terms of number of individuals were tenrecs (36%) and lemurs (26%), and in terms of biomass, bushpigs (65%) and lemurs (13%). In the austral winter proportionally more bushpigs, tenrecs, and lemurs were consumed as they are targeted at this time of year.

Even though wild terrestrial animals contribute a relatively small proportion of animal protein to the overall diet, these animals are broadly consumed; that is, many people eat them. Golden and colleagues working in the Makira region found hunting of lemurs to be unsustainable while acknowledging that removing this source of animal protein, whether through wildlife depletion via overhunting or through legal intervention, would diminish health and livelihoods of the local population (Golden, 2009; Golden et al., 2011). Jenkins et al. (2011), working in the Aloatra-Mangoro region, found that 95% of individuals reported having eaten protected species at some point in their lives and 44.5% had eaten 10 or more legally protected species over their lifetime. Likewise, in a village on the Masoala Peninsula 89% of households had consumed lemurs during their lifetime and 36% had eaten them during the prior year (Borgerson et al., 2016). Local extirpation of lemur species has been documented in recent decades in connection with this broad, shallow pattern of consumption (e.g. Gardner & Davies, 2014).

From the various bushmeat studies cited above, it is clear that wild animals are hunted throughout Madagascar irrespective of protected status. Endangered taxa are sometimes sheltered from exploitation by taboos, known as *fady* in Malagasy (referring to a system of ritualized regulation obeyed by individuals or families for moral or spiritual reasons). However, some have suggested that traditional taboos against hunting certain wild species (e.g. *Indri*) may be breaking down due to rapid social change, such as migration associated with artisanal goldmining (Jenkins et al., 2011; Jones et al., 2008). But as Golden and Comaroff (2015) note, "Madagascar is no stranger to massive religious, economic, and social transformation," and based on

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protracted study near Makira Natural Park, they find erosion of wildlife consumption taboos to be more complex and to occur at low rates, if at all, mediated differentially by migration, modernization, and the spread of Western religion. Whether taboos buffer wildlife extinctions or not, domestic meats are preferred over wild meats in many parts of Madagascar (Gardner & Davies, 2014; Jenkins et al., 2011; Merson et al., 2019; Randrianandrianina et al., 2010; Reuter et al., 2016b).

In light of the above factors we are impelled to ask why lemurs and other endangered species are hunted, both in the present and the past. Taking the remote Masoala Peninsula in northeastern Madagascar as an example once again, factors that appear primarily responsible for lemur hunting today are poverty, poor health, and child malnutrition. Knowledge of laws prohibiting lemur hunting has no appreciable impact, nor does level of education, involvement in ecotourism, traditional cultural values, taste preferences, opportunism, or human–wildlife conflict (Borgerson et al., 2016). In other regions of Madagascar poverty and resultant food insecurity also drive consumption of protected species (Borgerson et al., 2018; Golden et al., 2011, 2014; Jenkins et al., 2011; Merson et al., 2019; Reuter et al., 2016b). Population viability analysis incorporating hunting rates of lemurs in Makira Natural Park show that harvest rates are unsustainable (Brook et al., 2019). While we lack the information required to conduct population viability analyses for extinct lemurs, oral histories and the archaeological and paleontological record provide evidence concerning when and why *Pachylemur* went extinct.

15.3 Extinct Animals, including *Pachylemur*, Appear in the Oral History of Madagascar

There are numerous stories of hippopotamuses in ethnohistoric records and folklore of Madagascar (e.g. Burney & Ramilisonina, 1998; Dandouau, 1922; Godfrey, 1986), some of which involve killing. Stories of giant lemurs are less common, but they occur. Etienne de Flacourt (1661) recorded the existence of a large lemur called the *tretretretre* that purportedly still lived in the late 1600s in the region of Fort Dauphin (Tolognaro). This animal appears to match the sloth-like *Palaeopropithecus* (Mahé & Sourdat, 1972; Godfrey & Jungers, 2003). Other tales of giant lemurs describe different taxa, probably *Archaeolemur* (Burney & Ramilisonina, 1998) and *Pachylemur*. The latter is connected with tales of the *kisoala*, which translates literally to "knife of the forest." Descriptions of this animal were recorded by C. Borgerson (pers. comm.) on the Masoala Peninsula in northeastern Madagascar in 2011 and 2012.

On August 1, 2011, Borgerson interviewed eight male trappers each of whom was over the age of 60 at the time. Each had heard of the *kisoala*, but none had seen it. They said that it dwells in the largest of trees, and is too big to use the small peripheral branches. It climbs to the top, where it sleeps until foraging begins at dusk. Its claws are sharp and its call as loud as thunder; this is why the animal is called *kisoala* (*kiso* = knife, *ala* = forest). One of the trappers made a sound like a long continual "kiiiiiiiiiing" while everyone else nodded and affirmed "like a knife." They knew three men from the next village to the north, now deceased, who had long ago

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seen the animal in the interior of the forest when they were collecting *bilahy* bark. These men had encountered the animal in the dark; they were frightened so they ran and hid. The next day they searched for the *kisoala*, at first unsuccessfully, so they put a hat on a spear, sharp end up, to mark the place of their sighting. When they returned later that evening, they found the *kisoala* skewered on the weapon. It had mistaken the hat for a person, and had impaled itself by jumping onto the hat. The trappers claimed that the animal was much larger than *Varecia rubra* and had larger, more pointy ears. Most said it was greyish-black, and some noted that its fur reddened toward the hands and tail. Its arms and legs were roughly equal in length. They added that there was, still living, an old man who had seen the *kisoala*. His hamlet was about a week's walk from the trappers' village.

On January 31, 2012, Borgerson visited the old man, who affirmed that he had indeed seen a *kisoala*. Pointing to some mountains above his hamlet, he said the big lemur used to live there. It had red eyes and a call so loud that it hurts your ears (like a machete hitting metal). It would sleep high in the canopy during the day and forage at dusk. The old man said he had seen the animal around 10 years earlier, maybe more (his family suspected that it had been at least 40 years). One morning, when he went to the forest to check his *laly*, he was surprised to see that it had snared a big quadrupedal lemur, much bigger than *Varecia* – approximately the size of a fosa (*Cryptoprocta ferox*) or slightly larger (ca. 9 kg). The animal's fur was *maintikintina* (blackish with light specks). He suspected the animal had only just been caught, as it was actively trying to escape. Terrified and amazed that a trap so small could snare the leg of an animal this big, the man ran away. When he returned, the animal was gone and the area around the trap was torn up. He never saw the *kisoala* again and stated that he never again wanted to.

15.4 Parallels between *Pachylemur* and Its Close Phylogenetic Relative *Varecia*

Pachylemur was the largest member of the family Lemuridae (11.5–13.4 kg, Jungers et al., 2008) and is widely recognized by paleoanthropologists as having been an arboreal frugivore (Federman et al., 2016; Godfrey et al., 2008, 2012). It was probably the most important disperser of large seeds on Madagascar (Richard & Dewar, 1991). It would have been less destructive to seeds than *Archaeolemur* spp. or *Daubentonia robusta*, frugivorous extinct lemurs with clear morphological specializations for seed predation (e.g. Godfrey et al., 2004, 2008, 2012). In contrast to extant indriids (e.g. sifakas), extant lemurids such as *Varecia* and *Eulemur* tend to swallow medium or large seeds whole or with minimal damage, and seeds passing through their guts have high germination success (Dew & Wright, 1998). These two lemur genera are Madagascar's most effective extant dispersers of medium or large seeds. At three times the body mass of *V. rubra* (2.1–3.6 kg, Dutton et al., 2008; Vasey, 2003) and *V. variegata* (2.5–4.8 kg, Baden et al., 2008), *Pachylemur* would have been able to disperse even larger seeds.

Pachylemur traits relayed in the above oral histories suggest that this animal resembled *Varecia* in its pelage coloration and aspects of its ecology, behavior, and

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reproduction. *Pachylemur* evidently shared *Varecia*'s tri-color pelage (red, black, and grey in *Pachylemur*/white in *Varecia*) and dwelled high in the canopy in the largest trees, as do *Varecia* who spend the majority of their time in mid-to-upper forest strata of (Vasey, Baden & Ratsimbazafy, 2022 and refs. therein). *Varecia* has an unusual suite of reproductive traits given its relatively large size and predominantly diurnal activity pattern, including the bearing of litters, nesting of altricial young, and an absentee parenting system (i.e. oral transport of young combined with infant stashing) (Vasey, 2007). On Masoala, trees selected for nesting and stashing young (x = 40 per litter) are the largest in the forest, even larger than those used for feeding (Vasey et al., 2018).

A prominent feature of the oral histories relayed above is the description of *Pachylemur*'s loud calls, which likewise distinguish variegated lemurs. *Varecia*'s "roar-shriek" chorus is a group advertisement call that likely facilitates dispersed intracommunity communication within large home ranges amid a fission–fusion social system (Vasey, 2000, 2007). Their highly aggressive antipredator behavior consists of mobbing accompanied by alarm calls that continue long after the stimulus (i.e., predator) has departed. Ground predators evoke "pulsed squawks" and aerial predators evoke "abrupt roars." In captive observations that included experiments employing live raptors, live mammals, and decoys, *Varecia* routinely approached, lunged at, and at times even pounced upon or struck these perceived threats during antipredator displays (Macedonia, 1993). These confrontational antipredator tactics are reflected in the trappers' tale of the *kisoala* dropping onto a spear covered by a hat. If *Pachylemur* shared *Varecia*'s suite of reproductive traits and if any of its loud calls were part of an antipredator display, then these confrontational tactics could be interpreted not only as an effect of large body size, but also as a consequence of bearing sessile young bound to nest and stash sites, which would prevent caregivers from fleeing predators without risking reproductive loss, as proposed for *Varecia* (Macedonia, 1993).

Pachylemur and *Varecia* shared a daily rhythm involving foraging at dusk. In the morning and late in the day *V. rubra* shows bimodal peaks in time spent feeding and traveling with rest predominating midday. For reproductive females these peaks grow significant during the four-month lactation period (Vasey, 2005). Aside from sharing a daily feeding rhythm near dusk, *Pachylemur* and *Varecia* appear, at first, to have had different activity patterns. The trappers' stories suggest *Pachylemur* was cathemeral (or nocturnal), whereas *Varecia* are primarily diurnal (e.g. Vasey, 2000, 2003 and refs. therein). In cathemeral species daily routines are performed under all light conditions, throughout the 24h light/dark cycle (Halle, 2006). Among arboreal mammals, small and large body sizes are closely associated with nocturnality and diurnality, respectively (Charles-Dominique, 1975). Therefore a fully nocturnal active-period would be unlikely in a large-bodied arboreal primate such as *Pachylemur*, especially when contrasted with the predominantly diurnal niche of its smaller-bodied relative *Varecia*. However, one of us (N.V.) has observed sporadic nocturnal activity in *V. rubra* over the course of many field seasons on Masoala (loud calls and travel). Low levels of night-time activity also characterize captive *Varecia*

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(Bray et al., 2017; Rea et al., 2014). Thus, cathemerality may very well be facultative in *Varecia*. And presumably the shared common ancestor of *Varecia* and *Pachylemur* would also have been facultatively cathemeral, in common with most extant lemurids (Curtis & Rasmussen, 2006; Tattersall, 2008).

Anatomical inference adds further insight concerning activity pattern reconstruction. As in other large subfossil lemurs, *Pachylemur*'s small orbital diameter signals diurnal activity, whether scaled relative to body size (Jungers et al. 2002) or its proxy – skull length (Martin 1990; Walker 1967). However, in contrast to similarly sized diurnal anthropoids (e.g. African apes), the subfossil lemurs appear to have had small optic canals, indicating comparatively low visual acuity under well-lit (i.e. diurnal) conditions (Jungers et al., 2002). An expanded interpretation, prompted by the twilight activity reported by the trappers, is that small optic canals underlie an adaptation among the large subfossil lemurs to *retain* visual sensitivity for activity in dim light. Small optic canals (a proxy for optic nerve size) indicate high retinal summation, an adaptation to low light levels. In retinas with high summation, there is typically a higher proportion of rod photoreceptor cells (linked to nighttime vision) versus cone photoreceptor cells (linked to daytime/color vision). Whereas each individual cone typically connects with a single nerve ganglion cell, several rods normally connect to one nerve ganglion (i.e., they undergo summation), which narrows the width of the fibers that form the optic nerve. This visual system configuration, a compromise, would have served *Pachylemur* well during both daytime and nighttime activity. We therefore conclude, based on both behavior and anatomy, that *Pachylemur*, like *Varecia*, was facultatively cathemeral.

15.5 When Did *Pachylemur* Go Extinct?

Pachylemur is known from virtually every part of Madagascar where extinct lemurs have been found, including, most recently, the northwest (Beanka) (Burney et al., 2020). We know from radiocarbon records compiled by Crowley (2010) that *Pachylemur* was geographically widespread and that it survived until at least ~1,000 years ago across most of Madagascar. It was present on the west coast at Andolonomby (1295 cal yr BP [calibrated years before present]) and in central Madagascar at Ampasambazimba (1178 cal yr BP). At Tsirave in south central Madagascar, it lived for several hundred years into the last millennium (Fig. 15.2). Indeed, there is indirect evidence of its survival, in pockets, until at least 500 years ago (Muldoon, 2010). Radiocarbon dates on *Megaladapis* and *Palaeopropithecus* from Ankilitelo Cave in southwest Madagascar cluster around this time, and Muldoon (2010) infers that the entire community of extinct lemurs whose bones were found in this cave may date to this period. That community included *Pachylemur*. On the basis of the small mammals also found there, Muldoon (2010) reconstructed the region as semiarid 500 years ago, not very different from today. *Pachylemur* was among the last survivors of the megafauna. Thus, even if humans arrived as recently as 1,500 years ago, and certainly if they arrived earlier, we can infer long temporal overlap for *Pachylemur* and humans on Madagascar.

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15.6 Why Did *Pachylemur* Disappear?

Various mechanisms have been posited for the demise of the megafauna of Madagascar. At one extreme lies the notion that the megafauna were hunted to extinction shortly after humans arrived (the blitzkrieg overkill hypothesis; Walker, 1967); at the other lies the notion that the megafauna succumbed to an island-wide drought that peaked ~1,000 to 950 years ago (Virah-Sawmy et al., 2010). The megafaunal crash peaked several hundred years earlier than this (Godfrey et al., 2019), thus *before* the proposed peak drought and *after* the arrival of humans – perhaps up to 9,000 years later (Hansford et al., 2018, 2020). Many species survived in small pockets for centuries following this initial, precipitous decline. If the megafaunal populations collapsed well after humans arrived, then any blitzkrieg model of rapid overkill is not viable.

But climate change is also a weak explanation of megafaunal decline and extinction on Madagascar. Recent paleoclimatological research has clarified two things: first, there have been major changes in hydroclimate since the Last Glacial Maximum (LGM) ~21,000 years ago (e.g. Scroxton et al., 2019) without negative consequences for megafauna; and second, that there was no island-wide drought ~1,000 years ago (Faina et al., 2021). Megafauna disappeared in regions that were both wet and dry, regardless of the local rainfall amount.

We are beginning to understand regional differences in hydroclimate during the Holocene. In northwestern Madagascar there is evidence of an early Holocene wet event (~8,200 years ago), coinciding with a wet period on the African mainland, and an extended mid-Holocene dry event (Voarintsoa et al., 2017; Wang et al., 2019). There was little exceptional about the rest of the record in the northwest, although there were wet/dry fluctuations and several small wet peaks at the time of the Little Ice Age of the northern hemisphere (Scroxton et al., 2017).

Other parts of Madagascar are less well-studied than the northwest, although the record for the southwest from the LGM onward is currently being analyzed in great detail (Dawson et al., 2020). This is the driest part of Madagascar, and the region most likely to suffer in the event of a severe drought. We know that as temperatures rose during the deglaciation period (post LGM) in the southwest, there were fluctuating wet and dry periods prior to the beginning of the Holocene (Scroxton et al., 2019). We also know that there was a prolonged drought during the late Holocene, beginning between 1,500 and 1,600 years ago and lasting 700 years. This drought appears to have impacted local plants and animals. However, it primarily affected the biota of the coastal region, some of which survived the drought by moving elsewhere (Faina et al., 2021).

Stalagmites from the northwest provide no evidence of a simultaneous late Holocene drought. A dramatic shift in regional vegetation from C3 woodland to C4 savannah did occur in northwest Madagascar at ~ 1,100 years ago, but this was during the wettest interval of the past 1,700 years in that region (Burns et al., 2016; Scroxton et al., 2017) and it occurred at around the time of the megafaunal collapse. The mid-Holocene drought ~4,000 years ago does not appear to have had any important

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negative impact on the megafauna, and the significant drought beginning ~1,600 years ago in the southwest appears to have had only local effects on the large-bodied animals (Faina et al., 2021), without ultimately causing their extinction.

Stable isotope ($\delta^{15}N$) values for radiocarbon-dated subfossil lemur bones also cast doubt on a major role for climate change in giant lemur extinction. Controlling for diet and salinity, $\delta^{15}N$ values in bone are correlated with habitat moisture; higher values occur in drier habitats. If increasing aridity were responsible for megafaunal decline, we would expect an island-wide increase in $\delta^{15}N$ values culminating in the highest values at the time of proposed maximum drought at ~1,000 years ago. Nitrogen isotope data are available for different taxa, so that each can be tracked independently, assuring that differences in diet do not confound the habitat moisture signal. Trends over time were tested for *Pachylemur* between 7,730 cal yr BP and 1,175 cal yr BP in the Central Highlands, and between 3,800 cal yr BP and 1,010 cal yr BP in the southwest (Crowley et al., 2017). Crowley et al. (2017) found no change in subfossil nitrogen isotope values in the more arid parts of Madagascar and a significant change ($p = 0.004$) in nitrogen values in the Central Highlands (but getting wetter over time!). Hixon et al. (2018) went one step further, examining $\delta^{15}N$ for specific amino acids rather than bulk collagen $\delta^{15}N$ values at a single site in south central Madagascar, Tsirave, from ~3,800 cal yr BP to ~800 cal yr BP. Specific amino acids provide better proxies for habitat aridity than bulk values, given the possible influence of variation in diet on the latter. These data also demonstrated no evidence that aridification contributed to the demise of *Pachylemur*. In summary, we cannot rule out climate as a factor impacting the megafauna of Madagascar, but it is unlikely to have had a major effect.

If climate change did not trigger the decline of megafaunal populations, then humans must have, even if blitzkrieg can be ruled out. Hints concerning what must have happened come from both archaeological and paleontological sites (Table 15.2). The earliest archaeological sites suggest that diverse economies existed, some of which (such as coastal fishing) depended minimally or not at all on exploitation of megafauna (Douglass et al., 2018). Elephant bird eggshells have been found in archaeological context at Tony, Velondiake on the coast of western Madagascar (Douglass et al., 2019a) but the middens contain no bones of megafauna. The earliest archaeological site where megafaunal bones have been found in clear archaeological context is Anja Cave in northern Madagascar (Douglass et al., 2019a; Table 15.2). The archaeological record also suggests that by 1,000 years ago, introduced domesticated animals had become primary sources of animal protein at sedentary sites. Megafaunal remains have not been found at large settlement sites such as Mahilaka in northwestern Madagascar, where urbanization grew as a product of an expanding Indian Ocean trade economy (Radimilahy, 1998).

No *Pachylemur* bones have been reported at archaeological sites. In contrast, as stated above, butchered bones of *Pachylemur* have been reported at a paleontological site, Tsirave (Fig. 15.3; Godfrey et al., 2019; Perez et al., 2005). Sustained exploitation over a period of ~100 years can be demonstrated at this site (Godfrey et al., 2019), but no artifacts were collected there and there is no direct evidence of human occupation

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Table 15.2 Direct evidence of early human interaction with megafauna, in archaeological context where indicated

What	When	Where	Source
Butchery of elephant bird, *Aepyornis maximus*	>10,000 years ago	Christmas River, south central Madagascar	Hansford et al. (2018)
Butchery of elephant bird, *Mullerornis modestus*	~6,000 years ago	Lamboharana, southwest Madagascar	Hansford et al. (2018)
Butchery of hippopotami	~4,000 years ago	Anjohibe, northwest Madagascar	Gommery et al. (2011)
Butchery of *Palaeopropithecus*	Beginning ~2,300 years ago	Taolambiby, south central Madagascar	Perez et al. (2005)
Aepyornis eggshell in archaeological context	Beginning just under 2,000 years ago	Tony, Velondiake, western Madagascar	Douglass et al. (2019a)
Butchery of hippopotami	Between 2,000 and 1,500 years ago	Ambolisatra and Lamboharana, southwestern Madagascar	MacPhee and Burney (1991)
Extinct lemur, *Palaeopropithecus* sp., in archaeological context	Beginning ~1,500 years ago	Anja Cave, archaeological site, northern Madagascar	Douglass et al. (2019a)
Butchery of *Archaeolemur*	~1,300 years ago	Manombo Toliara, southwestern Madagascar	Godfrey et al. (2019)
Butchery of *Pachylemur*	Beginning ~1,200 years ago	Tsirave, south central Madagascar	Godfrey et al. (2019)
Aepyornis eggshell in archaeological context	Beginning ~1,200 years ago	Talaky	Battistini et al. (1963)
Butchery of *Aepyornis*	Over 1,000 years ago	Ambolisatra, southwestern Madagascar	Hansford et al. (2018)
Remains of giant tortoise and megafauna in archaeological context	Beginning in the 10th century	Andranosoa	Rasamuel (1984)
Remains of giant tortoise and extinct lemurs in archaeological context	Late 11th century	Andavakoera Gorge	Dewar and Rakotovololona (1992)
Remains of extinct animals and *Aepyornis* eggshell in archaeological context	13th century	Lakaton'ny akanga	Dewar and Rakotovololona (1992)

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Figure 15.3 Left femur of an adult *Pachylemur insignis* from Tsirave (UA3059, Lamberton Collection), showing chop and cut marks made during disarticulation. Note the alignment of the cut marks on the medial and lateral condyles (modified from Perez et al., 2005).

at this site. We know nothing about the economy of the people at Tsirave just over 1,000 years ago, apart from the fact that they hunted *Pachylemur*.

This is typical of megafaunal butchery records at paleontological sites on Madagascar; that is, there is no record of archaeological context. Indeed, the lack of archaeological context has been used as a reason to question the butchery records themselves (e.g. Mitchell, 2020). In part, the absence of archaeological context at paleontological sites may reflect the fact that few paleontological sites were excavated by archaeologists. The butchered bones of *Pachylemur* at Tsirave were collected by paleontologist Charles Lamberton in the early 1930s. Radiocarbon dating of 41 subfossil *Pachylemur* at this site reveals a span of dates between 3,800 and 800 years, with a spike for a short period just before 1,000 years ago (Fig. 15.4). It is within this spike that all of the dated butchered *Pachylemur* bones fall. This suggests that Lamberton dug through a human occupation zone, without recognizing it as such (Godfrey et al., 2019). All dated butchered bones of megafauna are older than 1,000 years and most are from paleontological sites (Table 15.2).

We would argue that populations of *Pachylemur* and other megafauna did decline because of humans, but the story of their demise is not a simple one. Human economies are not monolithic, and it was not until the population of humans on Madagascar increased with the expansion of the Indian Ocean trade network (bringing more settlers, increased sedentarism, urbanization, and the introduction of an increasing number of domesticated plants and animals) that rapid megafaunal

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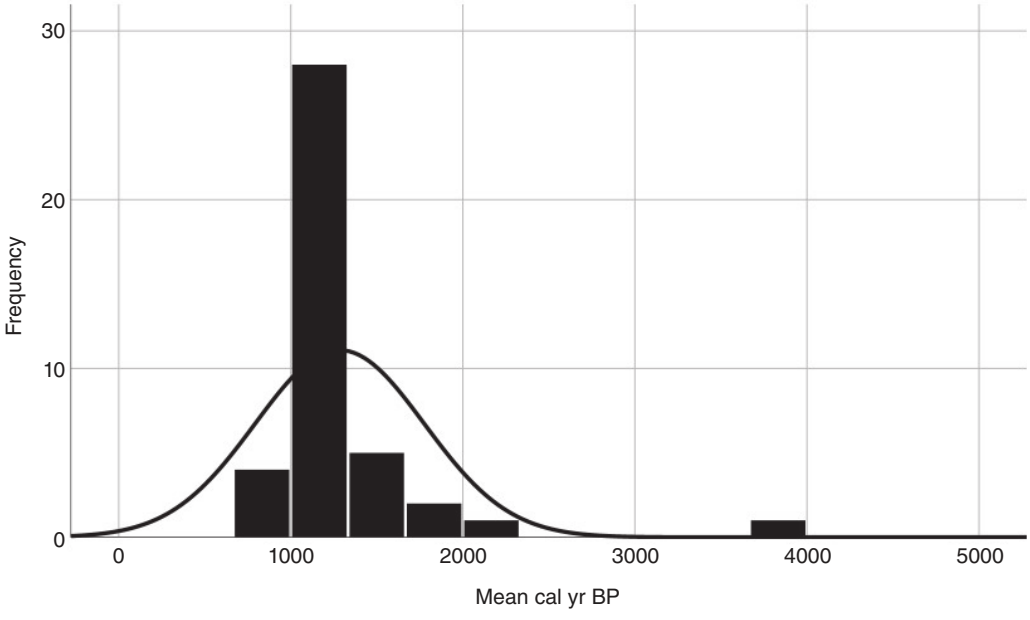

Figure 15.4 Distribution of 41 radiocarbon-dated bones of *Pachylemur* at Tsirave in south central Madagascar. All butchered bones fall in the spike in frequency just over 1,000 years ago, likely representing a human occupation zone.

decline occurred (Godfrey et al., 2019). It may seem counterintuitive that the megafauna would have declined as alternative sources of animal protein such as cattle were introduced to Madagascar, but domesticated animals support a larger human population than do wild animals, and human population size is a critical factor. Reflected globally in biomass distribution today, the biomass of humans at ≈0.06 gigatons of carbon (Gt C) and the biomass of livestock at ≈0.1 Gt C (dominated by cattle and pigs) far surpass that of wild mammals (≈0.007 Gt C) (Bar-On et al., 2018). Comparison of these values with estimates prior to the advent of humans indicate that while the total biomass of wild mammals (both marine and terrestrial) decreased by a factor of ≈6, the total biomass of mammals increased approximately fourfold (from ≈0.04 Gt C to ≈0.17 Gt C) due to vast increase of the biomass of humanity and its associated livestock (Bar-On et al., 2018).

Communities in the past, like communities in the present, were "not blanket consumers of all resources" (Douglass et al., 2019b). Researchers who model the persistence or decline of modern species around the world understand this complexity (Levi et al., 2011; Lu et al., 2010, 2011; Winterhalder & Goland, 1993; Winterhalder & Lu, 1997). Part of that complexity involves variation in the ways in which different species respond to humans and to habitat fragmentation, and variation in reproductive resilience and other aspects of species' life histories (Rahantaharivao et al., 2021). Wild animals vary in their tolerance of humans and human commensals. For some species, the mere presence of humans can elicit a costly predator-avoidance

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Figure 15.5 A reconstruction of *Pachylemur* by artist Joel Borgerson. Used by permission.

response, causing animals to flee even when fleeing reduces their access to resources and results in changes in foraging, ranging, and activity patterns (Frid & Dill, 2002). A recent meta-analysis of 76 studies has identified a systematic increase in nocturnality as a response of wild mammals to the rapid global expansion of human activity (Gaynor et al., 2018). This phenomenon may account for *Pachylemur*'s cathemeral (or possibly nocturnal) activity as reported by Masoala trappers.

While gaps remain concerning our knowledge of *Pachylemur*'s demise, we do know that it was a target of human predation and that its confrontational antipredator tactics (involving loud calls and possibly mobbing) made it highly conspicuous, and in turn more vulnerable to human weaponry. We also know that *Pachylemur* lived in regions that, because of habitat degradation, can no longer support a large-bodied, arboreal, frugivorous quadruped (Fig. 15.5). Likewise, degraded forest seems unable to support its highly frugivorous extant relative *Varecia* whose densities are greatly diminished or absent in such areas (Vasey et al., 2022). Cathemerality may have provided *Pachylemur* some protection from human predation, but frugivory, on the other hand, would have made this species more vulnerable to habitat

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fragmentation due to the spatial distribution and patchiness of fruit, as Janson (1992) has argued for primates generally. Habitat fragmentation has had a strongly negative effect on the occurrence of *V. variegata* in particular (Eppley et al., 2020) and this factor poses the most significant barrier to dispersal for the genus (Baden et al., 2014; Holmes et al., 2013). Habitat degradation and logging of large trees in Madagascar's eastern rain forests are considered major factors resulting in local extinctions of *Varecia*, not only because they rely heavily upon large, patchily distributed trees for fruit (Balko & Underwood, 2005; Borgerson, 2015; Herrera et al., 2011; Vasey, 2000, 2006), but more poignantly because they rely upon them for reproduction. *Varecia* are the only extant primates that build nests exclusively to care for young and the trees they select for nesting and stashing their non-clinging litters are the largest in the forest (Vasey et al., 2018). *Pachylemur*'s highly aggressive antipredator behavior suggests it may have possessed *Varecia*'s unusual suite of reproductive traits, demanding that they confront rather than flee from predators, tactics that would be selectively advantageous in protecting non-clinging, nested young. If so, *Pachylemur* would have shared the same grave vulnerabilities to local extinction as *Varecia*. On the basis of information currently available, we cannot know which human activities contributed the most to the demise of *Pachylemur*, but it is highly likely that both habitat degradation and hunting played a role.

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